43. Contributions to the Anatomy and Systematic Arrangement of the Cestoidea. By Frank E. Beddard, M.A., D.Sc., F.R.S., F.Z.S., Prosector to the Society.

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(Text-figures 1–6.)

XVIII. On *Tænia struthionis* (Parona) and Allied Forms.

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I have in my possession a considerable number of examples of a Cestode from the Ostrich *Struthio masaicus*, which are either identical with *Tænia struthionis* of Parona*, or belong to a closely allied species. The description given by Parona is not quite sufficient to enable the identity of his species and mine to be established beyond doubt. But it is at least clear, as I shall point out presently, by comparing the facts of structure one by one, that the species described by Parona and that to be described here by myself are not to be referred to the species described under the same specific name by v. Linstow †.

Although the details given by Parona are scanty, they are quite sufficient in my opinion to forbid any confusion between his species and that more fully dealt with by v. Linstow. My chief reasons for regarding them as two distinct species are the following. In the first place, v. Linstow's Cestode was obtained from *Struthio molybdophanes*; I infer that Parona obtained his worms from *Struthio camelus*. The scolex of *Tænia struthionis* of v. Linstow is only 1·18 mm. broad, while the species described by Parona has a stouter scolex of 2 mm. diameter ‡.

"Ein eigentliche Rostellum ist nicht vorhanden"—says v. Linstow of his species, while that described by Parona has, according to his figure, a quite strong rostellum. Correlated with this would appear to be the feebler character of the rostellar hooks in the worm from *Struthio molybdophanes*. The width of the proglottids in the two forms also appears to differ greatly; in the Tæniid described by v. Linstow, the diameter is but 4 mm.; while in Parona's specimens the same measurement was from 8 to 9 mm., *i. e.* quite double that of the first-named variety. This seems, like the other feature mentioned in

* Ann. Mus. Civ. Genova, (2 *a*) ii. 1885, p. 425.

† Arch. Mikr. Anat. xliii. 1893, p. 447.

‡ But see the observations of Zilluff quoted later (on p. 591) which tend to reduce the importance of this apparent difference, but do not affect what follows in the above *résumé*.

this brief account of differences, to be hard to reconcile with specific identity. The account given by Parona of internal structure is so slight that the comparison cannot be pursued further.

A question of nomenclature thus arises. The name *Tænia struthionis* first occurs in Rudolphi's "Synopsis"*, it is there a *nomen nudum*, but given on the authority of Houttuyn in Müller's edition of Linnæus†. In the earlier work of Rudolphi‡ the same worm (I presume) is named *Tænia struthiocameli*, and is also a *nomen nudum*, and again referred to Houttuyn in Müller's Linnæus §. I am indebted to Mr. C. Davies Sherborn for kindly informing me that Houttuyn himself‖ does not refer to the ostrich at all in his work, though Tænias are mentioned. It is thus erroneous to term the species *Tænia struthionis* or *Tænia struthiocameli* Houttuyn.

In Müller's work there is no name given at all; the occurrence of a *Tænia* in the ostrich being merely mentioned. Thus if a *nomen nudum* has any claim at all to be admitted, the species is to be referred to Rudolphi and is to be called *Tænia struthiocameli*, since the earlier of the two works by that author which mention the species calls it by that name. Diesing¶, however, quoting both Müller and Rudolphi's two works, terms the species *Tænia struthionis*, but again as a *nomen nudum*. The earliest actual description therefore of a *Tænia* from *Struthio* is that of Parona already referred to. We may perhaps safely accept his name, since it is accompanied by a description though not a conclusive one. I shall have to return again to this matter in considering the species to which it seems necessary to refer the worms which I now describe.

The *scolex* of the worm which forms the subject of the present communication is a little over 1 mm. in breadth in the two or three examples in which I measured it. The region of greatest breadth is opposite to the suckers; but the breadth was not increased by the extrusion of the latter. The suckers lay within the contour of the scolex. It is clear therefore that this species has a less robust scolex than Parona's *Tænia struthionis*. But while the actual measurements of the scolex of my species agree more with those of the worms described by v. Linstow as *Tænia struthionis*, my species shows a scolex with a well-developed rostellum, thus disagreeing with v. Linstow's worms and so far agreeing with that described by Parona. This is very evident from the figure given by Parona**, where the hardly extruded rostellum is plainly exhibited. Parona does not state the number

* Entoz. Syn. Mant. 1819, p. 173.
† Linné s Naturgeschichte von P. L. S. Müller, Th. vi. Bd. ii. p. 904.
‡ Entoz. Hist. Nat. 1810, p. 209.
§ It is to be noted that the initials of Müller are as stated here. He is referred o as "St. Müller" by Rudolphi, and "H. Müller" by Diesing.
‖ Natuurlyke Historie, vol. i. pt. 14, 1770.
¶ Systema Helminthum, i. 1850, p. 555.
** Parona, *loc. cit.* pl. vi. fig. 2.

of hooks present on the rostellum; v. Linstow gives the number found by himself as 180. I find in my species something between 120 and 130. These hooks are, as in other *Davainea*, of the well-known hammer-shape so characteristic of the family Davaineidæ.

The hooks really form two concentric rows, which arrangement is only clear in sections which pass through the "handle" part of the hook; that they are of different sizes is only shown in the "head" of the hammer, where one series is much shorter than the other; I could find no such difference in thickness in the "handle" region of the hooks. An alternation between larger and smaller hooks is stated by Parona to occur in his species. The hooks are of course implanted upon the edge of the circular rostellum. They are of the usual golden-brown colour. Von Linstow has represented the hooks of his examples, called by him *Tænia struthionis*, as being weak and frayed out at the point of implantation. I have found nothing of the kind in the robust (though small) hooks of the examples examined by myself.

My own observations are in fact more in accord with those of a later investigator than those referred to. Dr. Zilluff*, referring only to v. Linstow's paper and not to that of Parona, naturally finds differences to record ("naturally" if I am correct in thinking that v. Linstow's specimens are of another species than that which Parona and I describe). He emphasizes the rostellum and gives the diameter of the scolex as 1·33 mm., the dimensions agreeing with mine rather than with Parona's. But this author does not mention from what species of *Struthio* he obtained the material.

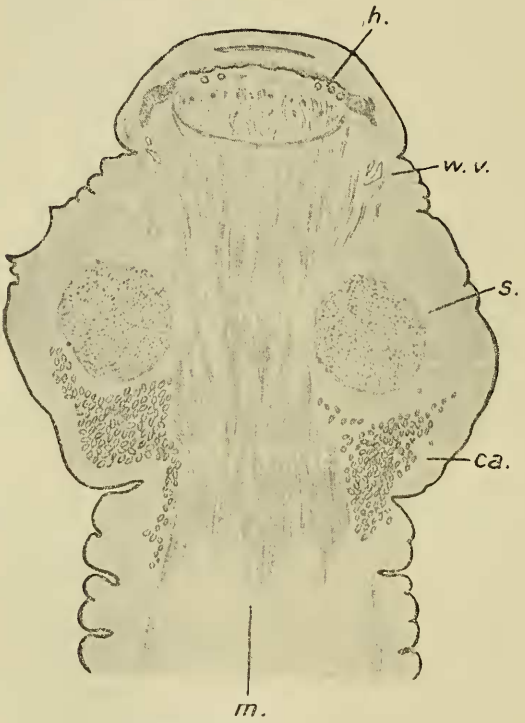
The *suckers* are not armed, as is the case in certain other members of the genus, a great part of the species of which have armed suckers. I believe that I can state this fact positively. Excepting where the retractor muscles are attached to the suckers, the latter lie for the most part free within the cavity of the scolex to which they are fitted. A space is generally visible between sucker and body-wall. Although there is no apparent difference that I could detect between the individual suckers, I have noted in this worm a means of distinguishing the dorsal from the ventral couple. The two dorsal vessels, instead of ending in the medullary region like the ventral vessels of the water-vascular system, bend dorsally, each of them perforating the layer of longitudinal muscles of the cortex ends in the neighbourhood of one of the suckers. The exact mode of ending I did not ascertain. It is therefore possible to distinguish two of the suckers as belonging to the dorsal surface. The characters of the musculature of the scolex I shall deal with later in

* "Vergleichende Studien über die Muskulatur des Skolex der Cestoden." Inaug.-Diss. Univ. Zürich, 1912. (Published also in Arch. f. Naturg. of the same year.) See also Lühe in Zool. Anz. xvii. 1894, p. 280.

connection with the general arrangement of the muscles of the body.

Von Linstow particularly mentions that in the species studied by himself, the anterior part of the body is devoid of calcareous bodies. In the specimens which I have examined by sections, the calcareous bodies are peculiarly numerous anteriorly, and especially in the scolex, where they form in parts closely aggregated masses as is shown in the accompanying sketch (text-fig. 1).

Text-figure 1.



Longitudinal section through scolex.

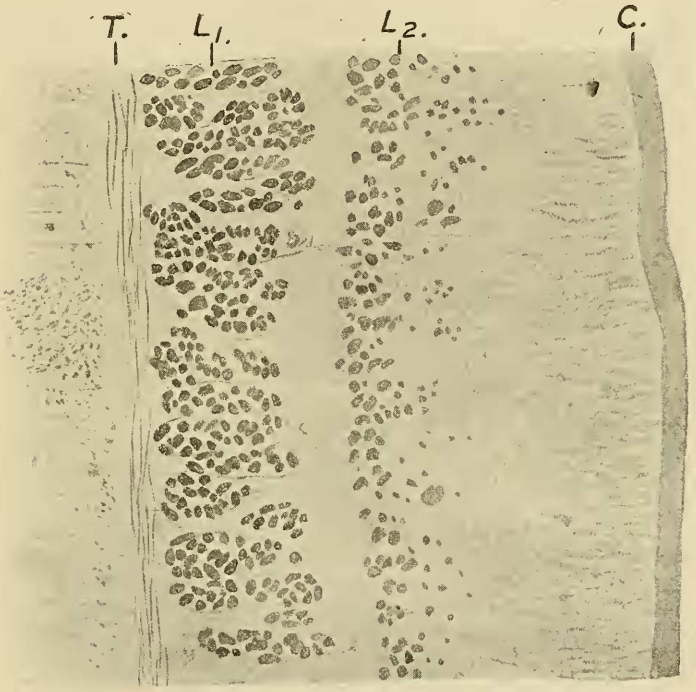
ca. Calcareous bodies. *h.* Hooks seen in transverse section through "root." *m.* Muscles of rostellum ending above in rostellum. *s.* Sucker. *w.v.* Water-vascular tubes.

I need not describe their distribution in the scolex exactly, for they occur everywhere between the outer skin and the suckers and rostellum, except, however, among the muscle-fibres of the longitudinal muscular layer. Further back in the neck region the medulla is largely occupied by masses of calcareous bodies

which are generally speaking very abundant in this species, so much so that I should be inclined to add the abundance of these bodies to any definition of the species. This is another reason for refusing to accept the identity of the worms from *Struthio masaicus* with those from *Struthio molybdophanes*.

The general shape of the body of this worm is as figured by Parona. The anterior region of the body is slender; it is much wider posteriorly, but not by any means so wide as in the species

Text-figure 2.



Part of a transverse section through a proglottid in anterior region of body.

C. Cuticle. L_1 & L_2. Layers of longitudinal muscles. *T.* Transverse muscles.

described by Parona. I found 5 mm. to be the greatest diameter of the posterior proglottids. They are overlapping, and as a rule so contracted as to be much wider than long. In a few cases the proglottids were, however, more expanded, but were never actually longer than broad. The worms reach a length of perhaps nine or ten inches.

The cortical layer is deep, the diameter being greater than

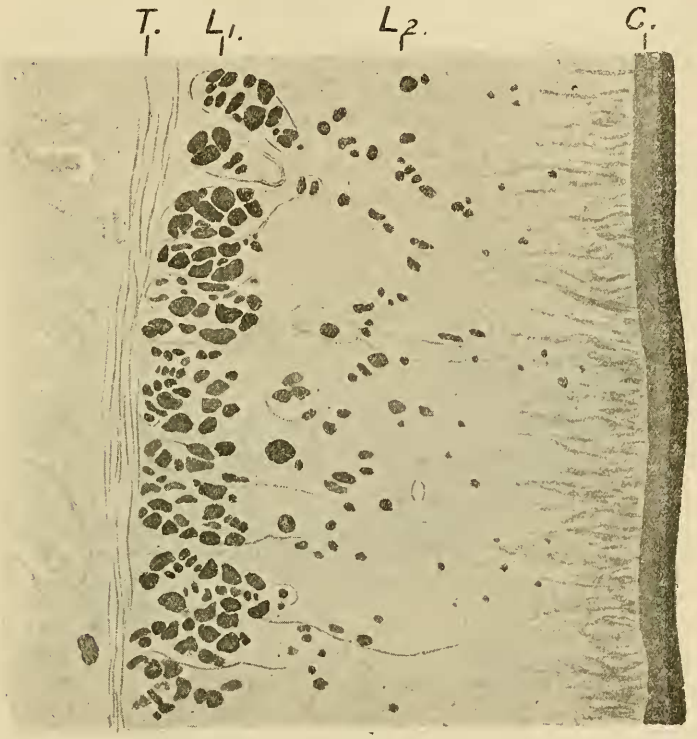
that of the medullary layer. This is particularly marked in the anterior segments, where the reproductive organs are only just beginning to appear. The *longitudinal muscle-layer* presents definite characters in the arrangement of its fibres, as is general among Cestodes. It is not usual to find accurate figures of the course of these fibres, which are constantly of systematic importance. I therefore attempt to reproduce here such accurate drawings.

At the base of the rostellum the longitudinal muscles lie in a continuous circular layer, in which form they are implanted upon the rostellum. A little further back, at the level of the suckers, the layer of muscles is markedly divided up into separate bundles which are of different sizes. There are 12 or 13 of these separate bundles which are more or less completely separated. In the neck, which immediately follows upon the scolex, the bundles cease to exist as separate structures except at the two sides opposite to the water-vascular tubes. The unsegmented or neck region in this worm is very short and, as in the other examples ascribed to the species *Tænia struthionis vel T. struthiocameli*, it may fairly be remarked that a neck can hardly be said to be present. Further back—but still in the anterior region of the body, where the gonads and their ducts are still only recognizable as a mass of condensed nuclei—the longitudinal muscular layer has more or less acquired its definitive arrangement. It is here (text-fig. 2) divisible into two quite distinct sheets. That nearest to the medulla consists of a row of bundles each consisting of a good number of individual fibres which are packed close together and separated by vertical fibres forming a dividing palisade. Above this is a very distinct space dividing the lower layer from the upper. This space is formed of ground-tissue, and there is no trace therein that I could discover of transverse muscle-fibres. On the outer side of this space is a layer of smaller bundles, *i. e.* each bundle consisting of comparatively few fibres, and above this again, without any marked interval, a certain number of single muscle-fibres, which complex reaches some way towards the subcuticular layer. Inside the whole longitudinal layer of muscles is a thin layer of transverse fibres separating these in the usual way from the medulla. Further back in the body the same arrangement exists, but it is not so clear cut as anteriorly. That is to say, the two layers of the longitudinal sheet are quite recognizable, but they are not so markedly divided from each other. This is shown in text-fig. 3.

Besides the sheets of muscle mentioned so far, the worm has, like most other Cestodes, a dorso-ventral system. I have already spoken of dorso-ventral fibres running between the bundles of the longitudinal coat. In addition to these the medulla is traversed by single fibres which cross it at right angles to its long diameter, and are numerous, dividing the medulla into quite narrow segments when seen in transverse sections.

The *water-vascular tubes* of this worm present no remarkable characters. The much larger ventral vessel is alone present in the posterior segments. Anteriorly both tubes are visible and superposed. The transverse trunks unite the ventrals in each segment. The usual valvular flaps in the ventral vessel are obvious and attached, as is usual (but not universal), to the inner wall of that tube.

Text-figure 3.



Part of a transverse section through a proglottid in the posterior region of the body.

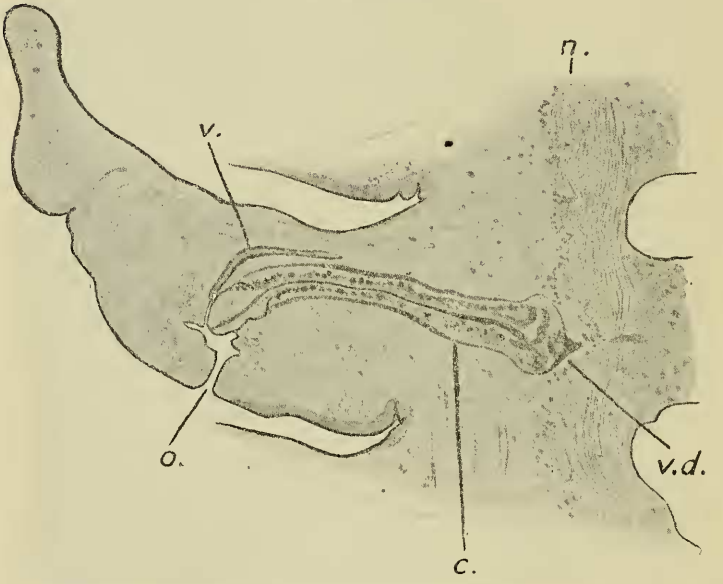
Lettering as in text-fig. 2.

The *male and female efferent ducts* open into a cloaca genitalis which is not specially deep. The genital pores are completely unilateral in this species, and somewhat anterior in position, at any rate in front of the middle line of the lateral border. I have found so many orifices in succession opening on to one side of the body, that I cannot believe that the conditions are for instance as in *Chapmania tauricollis*, where the orifices really

are alternate, though many open successively on to one side. All the pores that I found were on the same side of the body.

The *cirrus-sac* is comparatively short *, as in many species of *Davainea*, but not in all. It only just reaches the nerve-cord. It opens into the cloaca genitalis in front of and to one side of the vagina. The exact shape of the cirrus-sac has been carefully described in many Cestodes by many writers, and thus specific distinctions have been partly based upon its characters. The cirrus-sac of the present species shows that care must be taken in such descriptions. For I find considerable differences between the cirrus-sac in different segments, a state of affairs to be accounted for no doubt by varying contraction of its muscular walls.

Text-figure 4.



Longitudinal section through cirrus-sac (*c.*).

n. Nerve-cord. *o.* Orifice of genital cloaca. *v.* Vagina. *v.d.* Vas deferens.

More usually perhaps the cirrus-sac has the appearance represented in text-figure 4, which is drawn from a horizontal section through a more anterior segment. The cirrus-sac opens directly into the cloaca genitalis, and is of the same character and of pretty well the same diameter throughout. The walls are muscular but not thick; nor are they thicker in one region than in another. The vas deferens perforates the muscular coat at the extremity of the sac fairly exactly in the middle line, and is

* In extended proglottids the cirrus-sac lies obliquely, being directed forwards.

coiled within the sac. The cirrus, with which it is continuous, appears to run a straight course and not to be coiled, since it is shorter than the cirrus-sac. In some posterior segments the cirrus-sac presented a different appearance. The peripheral and greater part of the cirrus-sac is thicker-walled than a terminal rather spherical and wider region into which opens the vas deferens.

The cirrus-sac is ensheathed externally by a layer of rather large nucleated hyaline cells, a not unusual character.

Did these two forms of the cirrus-sac occur in different individuals, one would be tempted to see in them a specific difference.

The *vas deferens* presents an extensive coil after it issues from the cirrus-sac. This occupies quite one-third of the diameter of the segment when the latter is stretched laterally. The coils are at least mainly dorso-ventral in direction, since in horizontal sections the sperm-duct appears as a series of circular transversely cut areas.

The *vagina* has a straight or at most slightly sinuous course back to rather beyond the water-vascular tube—this section being thick-walled with a narrow lumen as in so many other Cestodes. A little way to the inside of the water-vascular tube the vagina narrows into an excessively fine bore, though with equally thick muscular walls at first. This slender region is coiled on the horizontal plane. It opens into the receptaculum seminis, which is rather pear-shaped. This and the succeeding portion of the vagina is not thick-walled but has a wider lumen, less of course in the case of the vagina. Although the proglottids, in which the vagina and its subdivisions had the characters that have just been mentioned, were not fully mature, at any rate as far as concerns the testes and sperm-duct, the receptaculum contained spermatozoa. It is necessary to point out that there is nothing to be specially remarked upon in the structure of the female efferent duct, which is constructed upon the plan usual in tapeworms. It is important, however, to be accurate, since there are minor differences to be noted which affect even the different species of *Davainea*.

Without attempting any general *résumé* for comparative purposes, I may direct attention to one or two species which differ from that now under consideration in these matters. In *D. sphecotheridis* of Johnston * there is apparently no distinct receptaculum seminis at all. In *D. corvina* Fuhrmann † the position of the receptaculum is different, beginning as it does to the outside of the water-vascular tube. In *D. polycalceola* ‡ the small receptaculum is close to the ovary. It is of further importance to note the age of the proglottid when giving the

* T. Harvey Johnston, "Second Report on the Cestoda and Acanthocephala collected in Greenland." Ann. Trop. Med. Parasit. iii. 1914, p. 107.

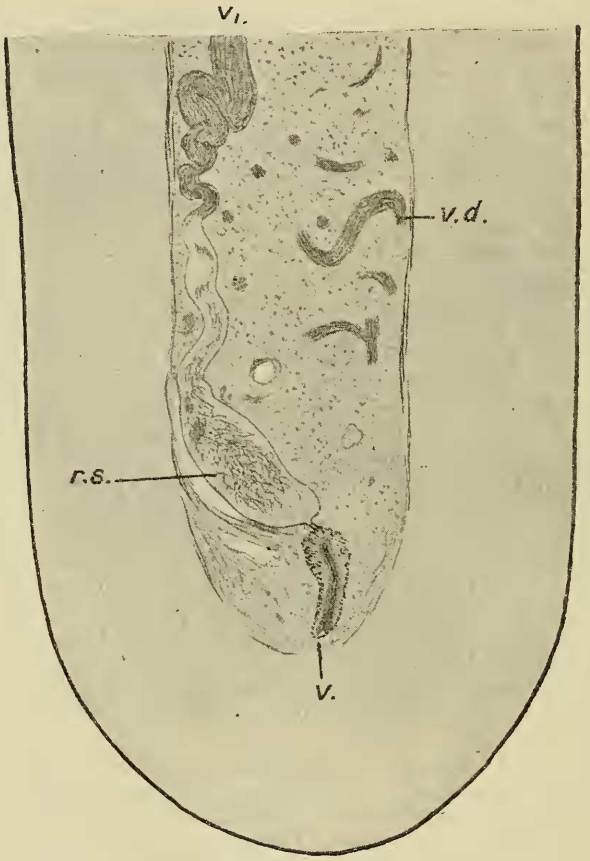
† Abh. Senck. Nat. Ges. xxxiv. 1911, p. 252, fig. 3.

‡ v. Janicki, "Ueber zwei neue Arten . . . . *Davainea*," Arch. de Parasit. vi. 1902, p. 265, fig. 5.

characters of the vaginal complex. The above description of that of "*Davainea struthionis*" relates to not fully mature proglottids. In fully mature proglottids the conditions observable are a little changed.

The female duct (see text-fig. 5) from the receptaculum seminis

Text-figure 5.



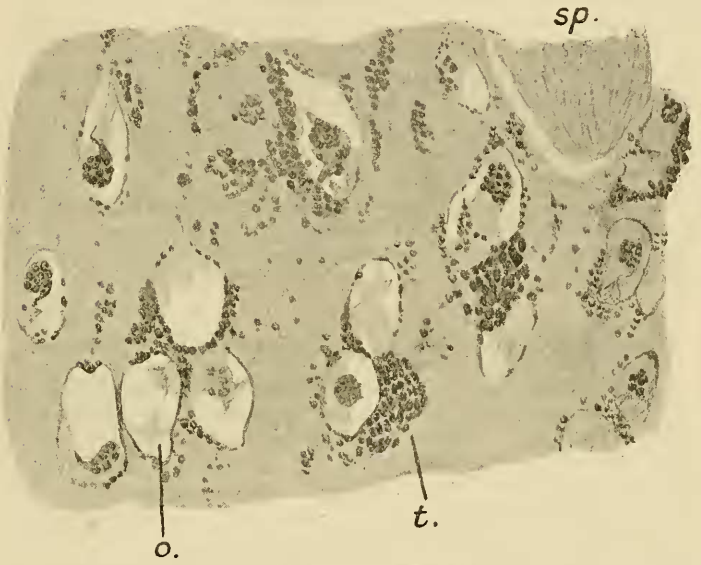
Part of transverse section through nearly ripe proglottid.

r.s. Receptaculum seminis. *v.*, v_1. Proximal and distal ends of vagina.
v.d. Vas deferens.

to its median end is gorged with sperm, and thus presents the appearance of an elongated receptaculum such as that referred to above in *Davainea corvina*. And, moreover, there is this further resemblance, that the vagina is pressed by its increasing

contents up to the margin of the water-vascular tube, occasionally crumpling up the latter before it. Nevertheless, the more dilated region is still distinguishable as the true receptaculum seminis. It is evident, therefore, that the differences apparently shown between species in the vagina must be handled with care. I may add that in fully mature proglottids the vagina appears to be continued onwards beyond its junction with the other tubes of the female system. This may be merely a burst, though in some cases it has a tubular character. It is here, I assume, that fertilization occurs.

Text-figure 6.



Ripe ova enclosed in capsules.

o. Capsule containing ovum. *sp.* Part of vagina gorged with sperm. *t.* Remains of a testes closely adpressed to an egg-capsule, the nuclei in the walls of which are represented.

The *uterus* in the genus *Davainea* is never a conspicuous structure and never, when it exists, does it persist long. It is, however, too much to say—as does Ransom *—that "a definite functional uterus is not developed." For in *D. aruensis* Fuhrmann † has described a uterus with a lining of cells and containing ripe ova, which uterus, however, rapidly disappears. The same appears to be the case with *D. microscolecina* and *D. corvina*,

* "The Tænoid Cestodes of North American Birds." Bull. U.S. Nat. Mus. No. 69, 1909, p. 14.

† Nova Guinea, vol. ix. Zoologie, Livr. 3, p. 169.

where the same author * remarks upon the rarity of observations upon the uterus of this genus. I find in the species with which I am here concerned very definite beginnings of a uterus, in which, however, I have not seen a large and continuous cavity. This consists in horizontal sections through proglottids, which are not fully mature but in which nevertheless the receptacula seminis are full of sperm, of a wide stretch of condensed medullary tissue. This structure appears to me to be exactly like the commencing uterus of some other Cestodes †. It lies in front of the ovary and shell-gland, but behind the receptaculum seminis and vas deferens, occupying thus about the width of the segment. It extends to a considerable distance right and left. The string of tissue representing the uterus is mainly to be differentiated from the surrounding medulla by its crowded nuclei. It is not solid but contains numerous cavities of various sizes. Some of these were filled with cells which may well be egg-cells. These cavities are at least frequently of the same size and shape as the oval interstices of the medullary meshwork. Later the proglottids (see text-fig. 6) are full of embryos each in its own separate cavity.

The following assemblage of characters are perhaps sufficient to define this species, to which I shall be unable to give a name with absolute certainty that it requires a new one. It will be better therefore to leave this matter unsettled for the present.

Definition of Davainea sp. *parasitic in* Struthio masaicus.

Length 10–14 *inches; greatest diameter of proglottids* 5 *mm. Scolex* 1·2 *mm. diameter, with double row of* 130 *hooks in all; suckers unarmed. Scolex and anterior part of the body abound with calcareous corpuscles, which also occur posteriorly. No neck present. Segments of body not longer than broad; ripe segments not moniliform. Genital pores unilateral. Cirrus-sac reaching to nerve-cord. Dorsal water-vessel absent from posterior region of body. Ova imbedded singly in parenchyma extending into cortex.*

The above will be sufficient pending a revision of the genus to place the species approximately.

General Remarks.

It is pretty clear from the foregoing observations upon the external characters and internal structure of this Cestode from *Struthio masaicus*, that it is certainly not to be confounded with the species named by v. Linstow *Davainea struthionis*, and which

* "Vogelcestoden der Aru-Inseln." Abh. Senck. Nat. Ges. xxxiv. 1911, p. 254, & fig. 4, p. 252.

† *Cf. e. g.* Beddard in the instance of *Chapmania tauricollis*, P. Z. S. 1915 p. 434, text-fig. 3.

is a parasite of another subspecies of *Struthio*, viz. *S. molybdophanes*. While the general dimensions and the relative size of the scolex seem to be much the same in v. Linstow's species and in my own, there are several salient features in which they disagree markedly. The scolex of v. Linstow's worm has no rostellum, in the species examined by myself the rostellum is strong: v. Linstow's species has no calcareous bodies in the scolex, while my species is peculiarly well provided with these bodies: whatever may be the interpretation of the "ovaries" of v. Linstow in the posterior segments of his species, whether they are really a divided uterus or paruterine bodies, that Cestode clearly differs from mine where the embryos are scattered each one in a cavity of its own: finally, if v. Linstow's representation of the cirrus-sac and the vagina opening quite separately prove correct, there is here a great difference from my species, where the relations between these ducts is quite normal. These facts are, as I think, sufficient to show that there can be no identity between the two Cestodes of *Struthio masaicus* and *Struthio molybdophanes* *.

On the other hand, an exact comparison of my species with that termed *Tænia struthionis* by Parona is more difficult. If we can trust as differential characters the diameter of the proglottids and the size of the scolex, then the two forms are different. There are no other data that seem to permit of a more definite expression of opinion.

* I have suggested (P. Z. S. 1915, p. 430) that v. Linstow's species may be actually referable to the genus *Chapmania*.